

which differ somewhat morphologically, represent independent origins of the allopolyploid or segregation from a once continuous distribution. *Clarkia epilobioides*, but not *C. modesta*, often occurs with *C. similis* in southern California. Both diploids are found in the area of *C. similis* in San Benito County.

#### ACKNOWLEDGEMENTS

The authors wish to acknowledge the loan of herbarium material from the following institutions: San Diego Museum of Natural History, California Academy of Sciences, Dudley Herbarium of Stanford University, Pomona College, University of California at Berkeley, Missouri Botanical Garden, United States National Herbarium, New York Botanical Garden and Gray Herbarium.

We are indebted to Professor Carl Epling for assistance with the Latin diagnosis.

Department of Botany,  
University of California, Los Angeles.

#### MORPHOLOGICAL CRITERIA FOR THE SPECIFIC VALIDITY OF *PINUS JEFFREYI*

DONALD A. JOHANSEN

The validity of *Pinus jeffreyi* Murr. as a distinct species has long been in dispute among taxonomists. Some (1, 2, 3, 7) recognize it as distinct; others consider it to be a variety of *P. ponderosa* Dougl. (5, 9); while still others give it no recognition whatever (10, 11). Those who reduce *P. jeffreyi* to varietal rank have apparently been disturbed by the fact that "intermediate" or "intergrading" forms are rather common in certain regions where the two species or others occur more or less intermingled. It was not until comparatively recently that it came to be realized that these "intergrades" are actually natural hybrids. Several such hybrids have been experimentally produced (4, and personal communications from Dr. Duffield).

Mirov (8) accepted the distinction between the two species on biochemical grounds and concluded that *P. jeffreyi* is phylogenetically older than *P. ponderosa*. In the latter conclusion, he agrees with the opinion of Lemmon (6).

For several years the writer has been conducting an intensive and extensive investigation of archegoniogenesis in the genus *Pinus* and other gymnosperms. Among other results, it was ascertained that the account of events within the archegonium, which has prevailed for the past fifty years, was incomplete. This story actually concerns only the almost entirely modern, evolved archegonium in a single species (the so-called

"*P. laricio*," whose true identity is now considerable of a mystery; it seems to have been a cultivated hybrid). Again, it was determined that each valid species possesses a mode of archegoniogenesis peculiar to itself; no two species out of twelve so far investigated follow the identical procedure. No species is wholly archaic nor entirely modern in all characteristics; in a given species certain archaic features are retained but all others are modern. It is the variation in the degree to which archaic features are retained that distinguishes any one species from the others. Consequently, a tabulation of all the archegonial characteristics prevailing in a given species serves as a reliable criterion for indicating differences between that species and any other species. Comparison of one character after another in each species reveals that *P. jeffreyi* differs so markedly from *P. ponderosa* that the only possible conclusion is that the former is a valid species.

In the following tabulation those characters known or at least presumed to be archaic are printed in italics.

Archegonial Character	<i>Pinus ponderosa</i>	<i>Pinus jeffreyi</i>
Number of archegonia	4 in very narrow ovules; 8 <i>in all others</i>	2 in narrow ovules 4 in wider ones
Location	<i>When 8, always in a complex</i>	Never in a complex
Shape	<i>Globoid to ovoid</i>	Laterally hemispheric
Neck cells	<i>Flush with outer cells of gametophyte and laterally elongated</i>	Deeply buried in gametophyte and vertically elongated; tending to obliteration
Jacket cells	Well developed	Poorly developed
Archegonial beak	Present	<i>Absent</i>
Chromatin elimination nucleus ("ventral cell") cut off	July 8-10; small; terminal	June 2-5; conspicuous; lateral; sometimes all chromatin is eliminated
Nuclear state	Always single; small	<i>Commonly binucleate</i> (two mitoses in place of one); quite large when single

Fertilization	Always single	<i>Always double when binucleate; otherwise single</i>
Syngamy occurs	July 20	June 10-12
Cytoplasm	<i>Turgid and highly vacuolate; does not plasmolyze</i>	Not turgid; few or no vacuoles; dense; always plasmolyzed after all killing fluids
Proteins or other stainable foods	<i>Absent</i>	Abundant and deeply stained
Nuclei in mature free-nucleate proembryo	Four	<i>Eight after double fertilization; otherwise four</i>
Reversion to Araucarian type of proembryo (walled)	Absent, or at least never observed	<i>Rather common</i>

Other interesting morphological features have turned up in other species but not in *P. jeffreyi* or *P. ponderosa*; they need not be mentioned here but they are useful in distinguishing these two from other species.

The ovules of *P. jeffreyi* are much larger than those of *P. ponderosa*. It is significant that binucleate archegonia, double fertilization and the tendency to revert to the ancestral (Araucarian) type of proembryo characterize species with large seeds (such as *P. lambertiana*), and that these features tend to disappear gradually as the ovules decrease in size until mostly evolved characters prevail in those species with the smallest seeds (as in *P. banksiana*). Large seeds occur in the cycads, *Ginkgo* and the Araucarians; the writer has recently found binucleate archegonia with double fertilization in *Zamia floridana*, as well as plurinucleate archegonia in *Ginkgo biloba* and twin proembryos in *Araucaria angustifolia*.

Natural hybrids in *Pinus* are still much of a morphological puzzle; the writer began to investigate them only during the past year. They are especially abundant in the region between Mountain Center and Idyllwild in the San Jacinto Mountains, with only *P. jeffreyi* occurring at the Mountain Center end and *P. ponderosa* at the Idyllwild end, with the hybrids in between and with numerous trees of *P. coulteri* and fewer of *P. flexilis* intermingled. Most of these hybrids more closely resemble *P. jeffreyi* in habit than they do *P. ponderosa*, but their archegoniogenesis resembles that of neither species. The suspicion, already voiced by others, is strong that *P. coulteri* has had something to do with the origin of these hybrids. Moreover,

at the far upper end of San Antonio Canyon, in the San Gabriel Mountains, there are numerous trees which have long been presumed to represent *P. ponderosa*, but their archegonial characters are so radically different from those of this species that they are either hybrids or constitute an unrecognized species. *Pinus lambertiana* is the only other species native to the neighborhood.

Mainly because of the presence of binucleate archegonia and double fertilization, together with the formation of Araucarian-like proembryos, all of which are pronouncedly archaic features, the writer is convinced that *P. jeffreyi* is the older species and therefore agrees with the conclusions of Lemmon and Mirov.

861 East Columbia Avenue  
Pomona, California

#### LITERATURE CITED

1. ABRAMS, L. R. Illustrated Flora of the Pacific States. Vol. 1. Stanford University, 1940.
2. BRADSHAW, K. E. Field characters distinguishing *Pinus ponderosa* and *Pinus jeffreyi*. Madroño 6: 15-18. 1941.
3. DALLIMORE, W. and A. B. JACKSON. A Handbook of Coniferae. London, 1948.
4. DUFFIELD, J. W. Relationships and species hybridization in the genus *Pinus*. Zeitschr. f. Forstgenetik u. Forstpflanzen 1: 93-100. 1952.
5. JEPSON, W. L. Manual of the flowering plants of California. Berkeley, 1923.
6. LEMMON, J. G. Revision of broken cone pines. Calif. State Bd. Forestry. 3rd Bien. Rept. 196-201. 1889-90. (Not seen; cited by Mirov.)
7. MARTINEZ, M. Los pinos mexicanos. 2nd. ed. Mexico, 1948.
8. MIROV, N. T. Phylogenetic relations of *Pinus jeffreyi* and *Pinus ponderosa*. Madroño 4: 169-171. 1938.
9. MUNZ, P. A. Manual of southern California botany. San Francisco, 1935.
10. SHAW, G. R. The genus *Pinus*. Publ. Arnold Arb. No. 3, 1914.
11. STANDLEY, P. C. Trees and shrubs of Mexico. Contr. U. S. Nat. Herb. vol. 23, part 1. 1920.

#### REVIEW

*A Natural History of Western Trees.* By DONALD CULROSS PEATTIE, illustrated by Paul Landacre. Houghton Mifflin Company, Boston, Mass. pp. xiv + 751, 4 maps (inside covers), 39 plates, 164 text figures. 1953. \$6.00.

It is hard to avoid superlatives in reviewing this handsome volume and, after all, why avoid them when they are so well-merited? Considering the wealth of information it conveys and its profuse and attractive illustration, it is a real bargain at the price fixed by the publishers. Anyone who is at all interested in trees will find that he is getting more than his money's worth when he purchases this book. Others who are not particularly concerned with trees, as such, will